The osteological development of four species of the Antarctic dragonfish (Pisces: Notothenioidei: Bathydraconidae)

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Voskoboinikova, O.S. 1998. The osteological development of four species of the Antarctic dragonfish (Pisces: Notothenioidei: Bathydraconidae). *Zoosystematica Rossica*, 7(1): 193-204.

The osteological development of four species of the family Bathydraconidae: *Psilodraco breviceps* (Gymnodraconinae), *Prionodraco evansii, Parachaenichthys georgianus* and *P. charcoti* (Bathydraconinae) has been examined with respect to the sequence of appearance of bones, morphogenesis and rate of ossification. Some considerable differences between *Prionodraco* and *Parachaenichthys* in the sequence of appearance of the ethmoidal bones and in morphogenesis of the neurocranium, splanchnocranium and pectoral fin are found. The rate of ossification in the bathydraconids in general is intermediate between those of the nototheniids and channichthyids. Comparison of the rates of differentiation of skeleton in these three families of the notothenioids suggests the paedomorph character of evolution of the suborder Notothenioidei as a whole.

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Investigations on the osteological development of antarctic fishes of the suborder Notothenioidei are directed to solution of some problems of systematics, phylogeny and evolution of this group (Voskoboinikova & Tereshchuk, 1991; Voskoboinikova, 1994; Voskoboinikova & al., 1994; Voskoboinikova & Kellermann, 1997). The importance of such a research is determined significantly by the fact that numerous osteological characters are used as the basis of classification of notothenioids (Eakin, 1981; Andersen, 1984; Balushkin, 1984; Iwami, 1985; Voskoboinikova, 1986; Balushkin, 1992; Balushkin & Voskoboinikova, 1995). The aim of this research is a comparative analysis of the osteological development of four species of bathydraconids of two subfamilies: *Psilodraco breviceps* Norman (subfamily Gymnodraconinae); *Prionodraco evansii* Regan, *Parachenichthys charcoti* (Vail.) and *P. georgianus* Fischer (subfamily Bathydraconinae).

Material, methods and terminology

The material used for this study belongs to the collection of larvae and juveniles of Antarctic fish of the Alfred Wegener Institute for Polar and Marine Research (Germany) made by A. Kellermann and W. Ekau, and to the collection of the Biological Station of Gdansk University (Poland) made by W. Slosarchyk and K. Skora. Some larvae were available through the Scientific Research Institute of Fishery and Oceanography (Russia) and were kindly provided by V.N. Efremenko. Series of 17 specimens (14.5-46.2 mm SL) of *P. breviceps*, 8 specimens (20.0-47.5 mm SL) of *P. evansii*, 19 specimens (20.5-60.0 mm SL) of *P. charcoti*, 15 specimens (23.8-76.0 mm SL) of *P. georgianus* and 3 specimens (44.0-47.0 mm SL) of *Gerlachea australis* Dollo were studied with the method by Potthoff (1984). Since I do not have day-to-day series, I refer to the standard length to identify ontogenetic stages. Drawings were made with a camera lucida attached to a stereo microscope. For the skull and pectoral girdle, the terminology of Harrington (1955) and Jollie (1986) was followed which is currently used in osteological works; for the axial and caudal skeleton, the terminology of Monod (1968) was adopted.

Table 1. The appearance of bones in ontogeny of *Psilodraco breviceps*

Bones	Standard length, mm								
	14.5	17.3	19.0	21.0	23.8	31.5	32.7	37.3	46.8
mesethmoideum	–	–	–	O	O	O	O	O	O
ant. lateral ethmoid	–	–	–	–	–	–	–	O	O
post. lateral ethmoid	–	–	–	–	O	O	O	O	O
frontal	–	O	O	O	O	O	O	O	O
nasal	–	–	–	O	O	O	O	O	O
parietal	–	–	–	–	O	O	O	O	O
vomer	–	–	–	O	O	O	O	O	O
parasphenoid	O	O	O	O	O	O	O	O	O
pterosphenoid	–	–	–	–	O	O	O	O	O
prootic	–	–	–	O	O	O	O	O	O
sphenotic	–	–	–	O	O	O	O	O	O
pterotic	–	O	O	O	O	O	O	O	O
epiothic	–	–	–	–	O	O	O	O	O
intercalar	–	–	–	–	–	O	O	O	O
posttemporal	–	O	O	O	O	O	O	O	O
supraoccipital	–	–	–	–	O	O	O	O	O
exoccipital	–	O	O	O	O	O	O	O	O
basioccipital	O	O	O	O	O	O	O	O	O
maxilla	O	O	O	O	O	O	O	O	O
premaxilla	O	O	O	O	O	O	O	O	O
dentary	O	O	O	O	O	O	O	O	O
articular	O	O	O	O	O	O	O	O	O
angular	O	O	O	O	O	O	O	O	O
palate	–	–	–	O	O	O	O	O	O
quadrate	O	O	O	O	O	O	O	O	O
ectopterygoid	–	–	O	O	O	O	O	O	O
mesopterygoid	–	–	O	O	O	O	O	O	O
metapterygoid	–	–	O	O	O	O	O	O	O
hyomandibular	–	–	–	O	O	O	O	O	O
symplectic	O	O	O	O	O	O	O	O	O
interhyal	–	–	–	–	O	O	O	O	O
epihyal	–	–	–	O	O	O	O	O	O
ceratohyal	O	O	O	O	O	O	O	O	O
upper hypohyal	–	–	–	–	–	–	–	O	O
lower hypohyal	O	O	O	O	O	O	O	O	O

Bones	Standard length, mm								
	14.5	17.3	19.0	21.0	23.8	31.5	32.7	37.3	46.8
basihyal	–	–	–	–	–	–	O	O	O
urohyal	–	–	–	O	O	O	O	O	O
basibranchial 1	–	–	–	–	–	–	–	–	–
basibranchial 3	–	–	–	–	–	–	–	O	O
hypobranchial 1	–	–	–	–	O	O	O	O	O
hypobranchial 2	–	–	–	–	O	O	O	O	O
hypobranchial 3	–	–	–	–	–	O	O	O	O
ceratobranchials	–	O	O	O	O	O	O	O	O
epibranchial 1	–	–	–	–	–	O	O	O	O
epibranchial 2	–	–	–	O	O	O	O	O	O
epibranchial 3	–	–	–	O	O	O	O	O	O
epibranchial 4	–	–	–	O	O	O	O	O	O
pharyngobranchial 2	–	–	–	O	O	O	O	O	O
pharyngobranchial 3	–	–	–	O	O	O	O	O	O
pharyngobranchial 4	–	–	–	–	O	O	O	O	O
opercle	O	O	O	O	O	O	O	O	O
preopercle	O	O	O	O	O	O	O	O	O
interopercle	–	O	O	O	O	O	O	O	O
subopercle	–	O	O	O	O	O	O	O	O
lacrimal	–	O	O	O	O	O	O	O	O
dermosphenotic	–	–	–	–	–	O	O	O	O
infraorbital 4	–	–	–	–	–	O	O	O	O
cleithrum	O	O	O	O	O	O	O	O	O
coracoid	–	–	–	–	O	O	O	O	O
scapula	–	–	–	–	–	–	O	O	O
radial 2	–	–	–	–	–	O	O	O	O
radial 3	–	–	–	–	O	O	O	O	O
radial 4	–	–	–	–	O	O	O	O	O
radial 5	–	–	–	–	–	–	O	O	O
supracleithrum	–	O	O	O	O	O	O	O	O
urostyle	–	O	O	O	O	O	O	O	O
hypural 1 + 2	–	O	O	O	O	O	O	O	O
hypural 3	–	O	O						
hypural 4	–	–	O						
hypural 3 + 4				O	O	O	O	O	O
epurals	–	–	–	–	–	O	O	O	O

Results

The four examined species of bathydraconids differ from each other and from the species of the more primitive family Nototheniidae in the sequence of appearance and morphogenesis of certain bones, as described below.

The sequence of appearance of bones. In general, all species reveal similar sequence of appearance of bones (Tables 1-3). Data on *P. charcoti* are not included in the table because they are similar to those on *P. georgianus*. The most significant difference has been found in the appearance of the ethmoidal bones and branchials. In *P. breviceps*, the mesethmoid and posterior lateral ethmoid appear almost simultaneously, and the anterior lateral ethmoid occurs later. In *P. evansii*, first the mesethmoid, and later the lateral ethmoids appear. Species of *Parachaenichthys* show a similar sequence of appearance of the mesethmoid and posterior lateral ethmoid, but there is a long interval

Table 2. The appearance of bones in ontogeny of *Prionodraco evansii*

Bones	Standard length, mm						
	20.0	24.5	25.0	26.7	36.5	41.0	47.7
mesethmoideum	–	–	–	–	–	O	O
ant. lateral ethmoid	–	–	–	–	–	–	O
post. lateral ethmoid	–	–	–	–	–	–	O
frontal	O	O	O	O	O	O	O
nasal	–	–	–	–	O	O	O
parietal	–	–	–	–	O	O	O
vomer	–	–	O	O	O	O	O
parasphenoid	O	O	O	O	O	O	O
pterosphenoid	–	–	–	–	–	O	O
prootic	–	–	–	–	–	O	O
sphenotic	–	O	O	O	O	O	O
pterotic	–	O	O	O	O	O	O
epiothic	–	–	–	O	O	O	O
intercalar	–	–	–	–	–	O	O
posttemporal	O	O	O	O	O	O	O
supraoccipital	–	–	–	–	O	O	O
exoccipital	–	O	O	O	O	O	O
basioccipital	–	O	O	O	O	O	O
maxilla	O	O	O	O	O	O	O
premaxilla	O	O	O	O	O	O	O
dentary	O	O	O	O	O	O	O
articular	O	O	O	O	O	O	O
angular	O	O	O	O	O	O	O
palate	–	–	–	–	O	O	O
quadrate	O	O	O	O	O	O	O
ectopterygoid	–	–	–	–	O	O	O
mesopterygoid	–	O	O	O	O	O	O
metapterygoid	–	O	O	O	O	O	O
hyomandibular	–	–	–	–	O	O	O
symplectic	–	O	O	O	O	O	O
interhyal	–	–	–	–	O	O	O
epihyal	–	–	–	–	O	O	O
ceratohyal	–	O	O	O	O	O	O
upper hypohyal	–	–	–	–	–	–	–

Bones	Standard length, mm						
	20.0	24.5	25.0	26.7	36.5	41.0	47.7
lower hypohyal	–	–	–	–	O	O	O
basihyal	–	–	–	–	–	O	O
urohyal	–	–	–	–	O	O	O
basibranchial 1	–	–	–	–	–	–	O
basibranchial 3	–	–	–	–	–	O	O
hypobranchials 1–3	–	–	–	–	–	O	O
ceratobranchials 1–5	–	O	O	O	O	O	O
epibranchials 1–4	–	–	–	–	O	O	O
pharyngobranchials 2–4	O	O	O	O	O	O	O
opercle	O	O	O	O	O	O	O
preopercle	O	O	O	O	O	O	O
interopercle	–	O	O	O	O	O	O
subopercle	–	O	O	O	O	O	O
lacrimal	–	–	O	O	O	O	O
dermosphenotic	–	–	–	–	O	O	O
infraorbital 1	–	–	–	–	–	–	–
infraorbital 2	–	–	–	–	–	–	–
infraorbital 3	–	–	–	O	O	O	O
infraorbital 4	–	–	O	O	O	O	O
cleithrum	O	O	O	O	O	O	O
coracoid	–	O	O	O	O	O	O
scapula	–	–	–	–	O	O	O
radial 2	–	–	–	O	O	O	O
radial 3	–	O	O	O	O	O	O
radial 4	–	O	O	O	O	O	O
radial 5	–	–	–	–	O	O	O
supracleithrum	O	O	O	O	O	O	O
urostyle	–	O	O	O	O	O	O
hypural 1 + 2	–	O	O	O	O	O	O
hypural 3	–	–	–	O			
hypural 4	–	–	–	O			
hypural 3 + 4					O	O	O
hypural 5	–	–	–	–	O	O	O
epurals	–	–	–	–	O	O	O

between the appearance of the posterior and anterior lateral ethmoids, the last bone being not found in the available larvae and juveniles of *P. charcoti.* Apparently, the noted delay is responsible for the subsequent reduction of this bone in adults of *Parachaenichthys.* In *P. breviceps* and *P. evansii,* the mesethmoid occurs as single bone (Fig. 1), but in species of *Parachaenichthys* and *G. australis* there are two distinct centres of ossification of the mesethmoid: at the anterior end of the snout, and between anterior ends of the frontals (Fig. 2c), which later join to one bone.

In *Psilodraco* and *Prionodraco,* the epibranchials appear earlier than the hypobranchials, and in *Parachaenichthys* these elements occur simultaneously.

As compared to the nototheniids (Voskoboinikova & Kellermann, 1997), heterochronies have been revealed in the appearance of the ethmoidal bones, some elements of the palatoquadrate and hyoid arches of the splanchnocranium, and caudal skeleton. In the nototheniids, both ethmoidal bones appear, as a rule, later than most of other bones of the neurocranium, but unlike to the bathydraconids, the lateral ethmoid appears

Table 3. The appearance of bones in ontogeny of *Parachaenichthys georgianus*

Bones	Standard length, mm								
	25.7	34.0	38.2	43.0	47.0	49.0	51.0	68.9	76.0
mesethmoideum	–	–	O	O	O	O	O	O	O
ant. lateral ethmoid	–	–	–	–	–	–	–	–	O
post. lateral ethmoid	–	–	–	–	O	O	O	O	O
frontal	O	O	O	O	O	O	O	O	O
nasal	–	–	–	O	O	O	O	O	O
parietal	–	–	–	O	O	O	O	O	O
vomer	–	O	O	O	O	O	O	O	O
parasphenoid	O	O	O	O	O	O	O	O	O
pterosphenoid	–	–	–	–	O	O	O	O	O
prootic	–	–	–	O	O	O	O	O	O
sphenotic	–	–	O	O	O	O	O	O	O
pterotic	O	O	O	O	O	O	O	O	O
epiotic	–	–	–	O	O	O	O	O	O
intercalar	–	–	–	–	O	O	O	O	O
posttemporal	O	O	O	O	O	O	O	O	O
supraoccipital	–	–	–	O	O	O	O	O	O
exoccipital	–	–	O	O	O	O	O	O	O
basioccipital	–	O	O	O	O	O	O	O	O
maxilla	O	O	O	O	O	O	O	O	O
premaxilla	O	O	O	O	O	O	O	O	O
dentary	O	O	O	O	O	O	O	O	O
articular	O	O	O	O	O	O	O	O	O
angular	O	O	O	O	O	O	O	O	O
palate	–	–	O	O	O	O	O	O	O
quadrate	O	O	O	O	O	O	O	O	O
ectopterygoid +	–	O	O	O	O	O	O	O	O
metapterygoid	–	–	O	O	O	O	O	O	O
hyomandibular	–	–	O	O	O	O	O	O	O
symplectic	O	O	O	O	O	O	O	O	O
interhyal	–	–	–	O	O	O	O	O	O
epihyal	–	–	O	O	O	O	O	O	O
ceratohyal	O	O	O	O	O	O	O	O	O
lower hypohyal	–	–	–	O	O	O	O	O	O
basihyal	–	–	–	O	O	O	O	O	O
urohyal	O	O	O	O	O	O	O	O	O
basibranchial 1	–	–	–	–	–	–	–	–	–
basibranchial 3	–	–	–	–	O	O	O	O	O
hypobranchials 1–3	–	–	–	–	O	O	O	O	O
ceratobranchials 1–5	O	O	O	O	O	O	O	O	O
epibranchials 1–4	–	–	–	–	O	O	O	O	O
pharyngobranchials 2–4	O	O	O	O	O	O	O	O	O
opercle	O	O	O	O	O	O	O	O	O
preopercle	O	O	O	O	O	O	O	O	O
interopercle	–	O	O	O	O	O	O	O	O
subopercle	O	O	O	O	O	O	O	O	O
lacrimal	O	O	O	O	O	O	O	O	O
dermosphenotic	–	–	–	O	O	O	O	O	O
infraorbital 1	–	–	–	–	–	–	–	–	–
infraorbital 2	–	–	–	–	–	–	–	–	–
infraorbital 3	–	–	–	O	O	O	O	O	O
infraorbital 4	–	–	O	O	O	O	O	O	O
infraorbital 5	–	–	–	–	–	–	–	–	–
cleithrum	O	O	O	O	O	O	O	O	O
coracoid	–	–	–	–	O	O	O	O	O
scapula	–	–	–	–	O	O	O	O	O
radial 2	–	–	–	–	–	–	–	–	–
radial 3	–	–	–	O	O	O	O	O	O
radial 4	–	–	–	O	O	O	O	O	O
radial 5	–	–	–	–	–	–	–	–	–
supracleithrum	O	O	O	O	O	O	O	O	O
urostyle	O	O	O	O	O	O	O	O	O
hypural 1 + 2	O	O	O	O	O	O	O	O	O
hypural 3	O	O							
hypural 4	O	O							
hypural 3 + 4			O	O	O	O	O	O	O
epurals	–	–	–	O	O	O	O	O	O

simultaneously with the mesethmoid, or even earlier. In the nototheniids, simultaneous or earlier appearance of the hyomandibular as compared to the meso- and metapterygoids was noted. In the bathydraconids, the hyomandibular appear later than pterygoids. Among the bathydraconids, the species of *Parachaenichthys* show the sequence of appearance of bones most similar to that of the channichthyids (Voskoboinikova, 1997). Differences between the channichthyids and species of *Parachaenichthys* are revealed in later appearance of the bones of hyoid arch, some bones of the neurocranium such as the supraoccipital, sphenoticum, prooticum, parietal, lateral ethmoid and mesethmoid. The teeth, infraorbitals, bones of the suspensorium, basi- and exoccipitals, vomer appear earlier in the channichthyids. The sequence of appearance of bony elements of axial skeleton in the bathydraconids is similar to that in the nototheniids and channichthyids. Fishes of all three families have two centres of ossification: from the anterior part of notochord posteriorly and from the urostyle posteriorly [except for *Pleuragramma antarcticum* Boul. which has three centres of ossification (Voskoboinikova & al., 1994)]. Osteological development of the skeleton of pectoral fin is similar to that in nototheniids and channichthyids. Four free pectoral radials appear, the

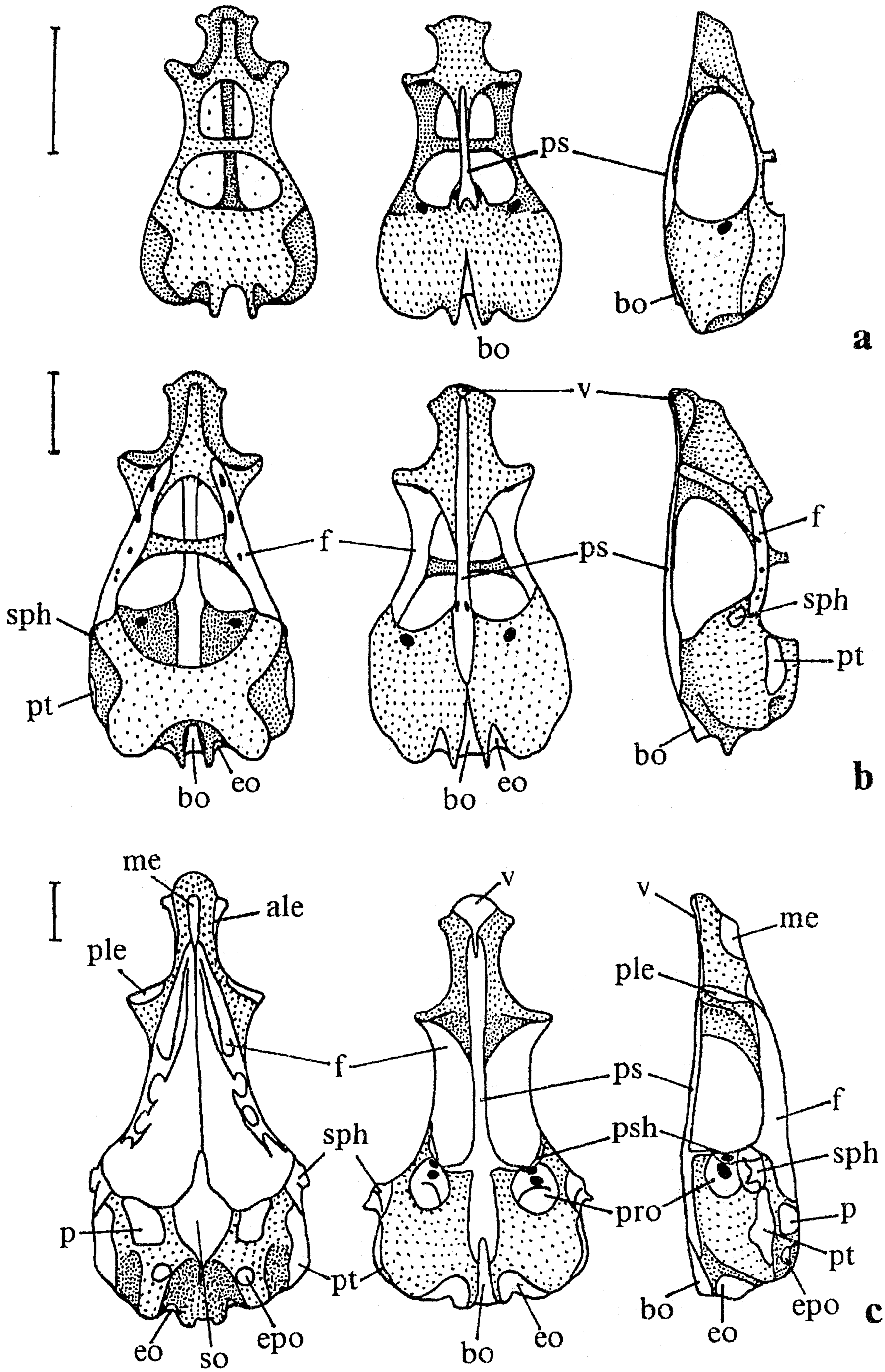

Fig. 1. Development of the neurocranium of *Psilodraco breviceps* showing dorsal, ventral and left lateral views. Standard lengths of specimens are: (**a**) 14.5 mm; (**b**) 23 mm; (**c**) 37 mm. Scale bar 1 mm. *ale*, anterior lateral ethmoid; *bo*, basioccipital; *eo*, exoccipital; *epo*, epiotic; *f*, frontal; *me*, mesethmoid; *p*, parietal; *ple*, posterior lateral ethmoid; *pro*, prootic; *ps*, parasphenoid; *pt*, pterotic; *psh*, pterosphenoid; *so*, supraoccipital; *sph*, sphenotic; *v*, vomer. Cartilage stippled, ossifying white.

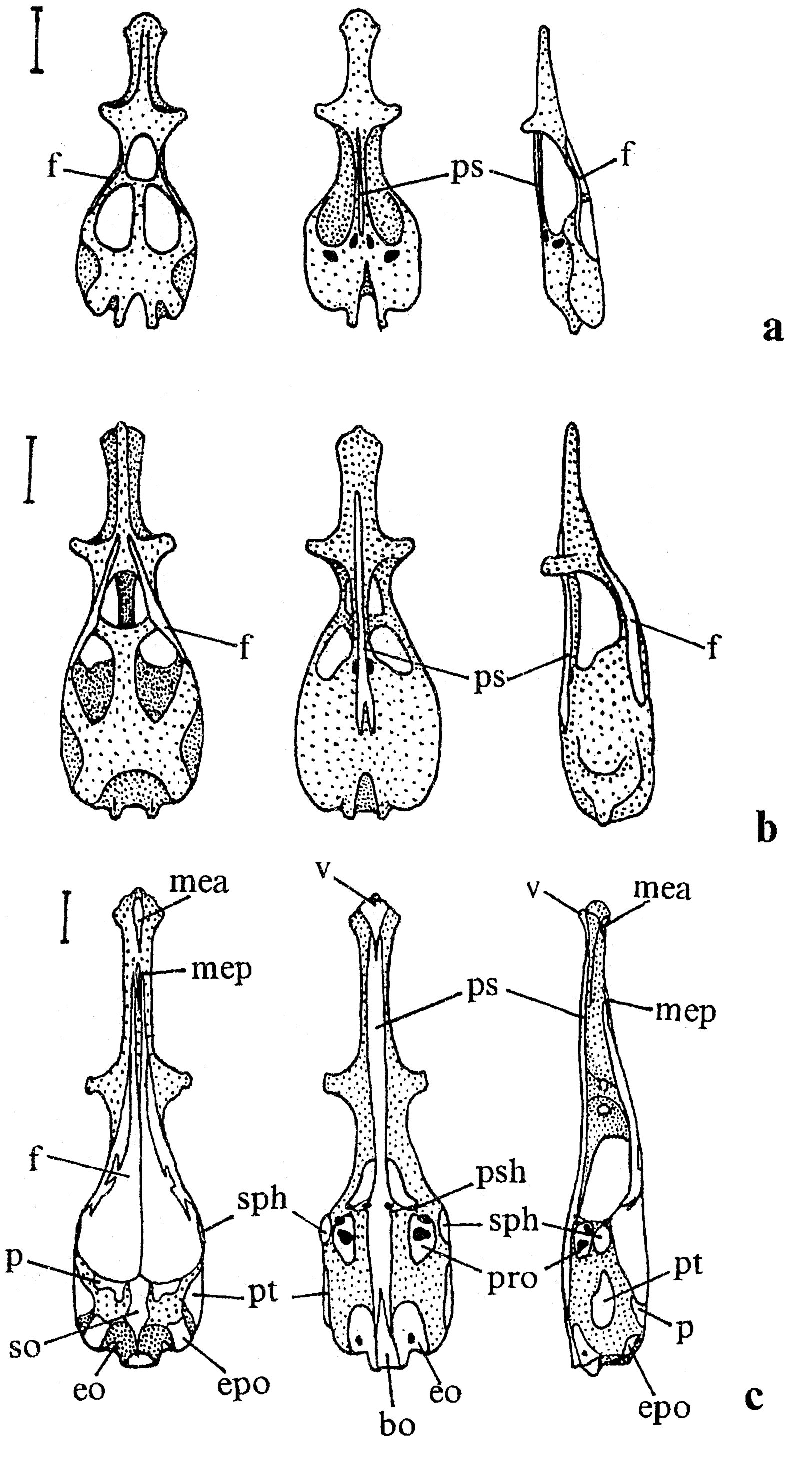

Fig. 2. Development of the neurocranium of *Parachaenichthys charcoti*. Standard lengths of specimens are: (a) 22.5 mm; (b) 26.0 mm; (c) 47 mm. Scale bar 1 mm. *mea*, anterior centre of the mesethmoid; *mep*, posterior centre of the mesethmoid. Other abbreviations as in Fig. 1.

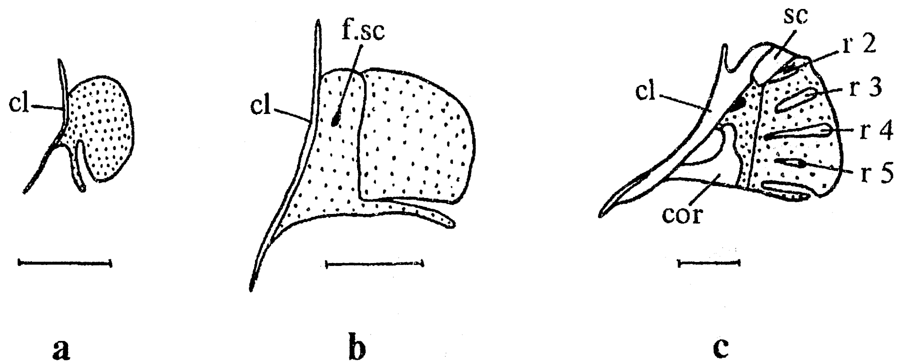

Fig. 3. Development of the pectoral girdle and pectoral radials of *Parachaenichthys charcoti*. Length of specimens as in Fig. 2. Scale bar 1 mm. *cl*, cleithrum; *cor*, coracoid; *f.sc*, scapular foramen; *r*, radial; *sc*, scapula.

uppermost of which (r 2, Fig. 3) later being joint to the scapula (Voskoboinikova & al., 1994). Osteological development of the caudal fin of the bathydraconids mostly repeats the development of the most advanced notothenids *Pleuragramma* and *Gobionotothen* which are characterized by acceleration of the development of this structure (Totton, 1914; Voskoboinikova, 1994; Voskoboinikova & Kellermann, 1997) as compared to other nototheniids. The ossification of the hypurals begins with appearance of a single bony hypural 1+2. The previously separated bony hypurals 3 and 4 later join in a single hypural 3+4. The hypural 5 occurs later in *Prionodraco* and *Parachaenichthys,* and disappears in *Psilodraco* (Andriashev & al., 1989) (Fig. 4).

Morphogenesis. At the early stages, all four species of the bathydraconids have the same compact shape of the neurocranium. *P. breviceps* (Fig. 1a) and *P. evansii* are characterized by a broad interorbital space and rather short ethmoidal region; *Parachaenichthys* (Fig. 2a) has a tight interorbital space and relatively long ethmoidal region. In first two species, the ethmoidal region and vault of the skull are high, and in *Parachaenichthys* they are low. Later, the lengthening of the skull and decreasing of its height proceed in all four species (Figs 1b, c; 2b, c). At the early stages, in all examined species of the bathydraconids, a rather deep notch on the posterior part of the cartilaginous endocranium is present which has also been found in the channichthyids and nototheniids (only in *P. antarcticum*) (Voskoboinikova & al., 1994). A comparison of morphogenesis of the neurocranium of nototheniids, bathydraconids, and channichthyids reveals, that, at the early stages, *Psilodraco* and *Prionodraco* are more similar to the most primitive nototheniid genera *Notothenia, Lindbergichthys* and *Gobionotothen* in the shape of neurocranium (Voskoboinikova & Kellermann, 1997), and *Parachaenichthys* is similar to the

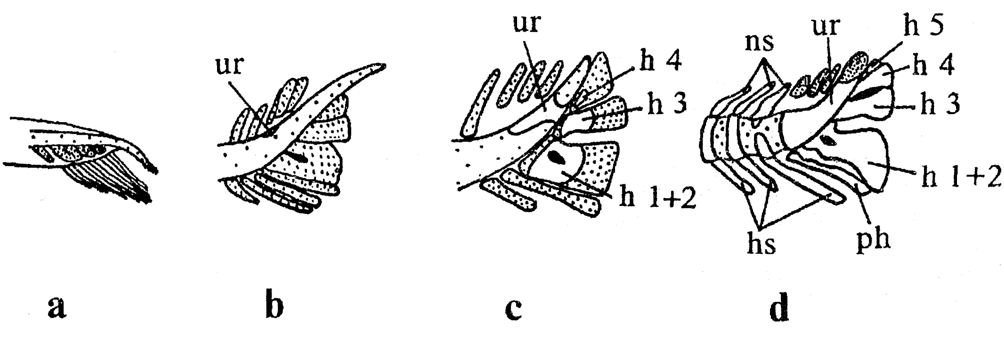

Fig. 4. Development of the caudal skeleton in *Parachaenichthys charcoti*. Lengths of specimens as in Fig. 2. Scale bar 1 mm. *hs*, haemal spine; *h*, hypural; *ns*, neural spine; *ph*, parhypural; *ur*, urostyle.

channichthyids. At the early stages, the structure of the splanchnocranium of the bathydraconids differs from that in the nototheniids in the larger length of the jaws, palatoquadrate, hyoid and gill arches which are the longest in *Parachaenichthys* being very similar to those of the channichthyids (Figs 5a, 6a). During ontogeny, in *Psilodraco* and *Prionodraco* the relative height of the suspensorium increases, and the length of the splanchnocranium decreases. In *Parachaenichthys*, the height of the suspensorium increases to a lesser extent, and the splanchnocranium remains very long. Probably, retardation of appearance of the hyomandibular in the bathydraconids results in the reduction of the ventral end of that bone. Consequently, the bone obtains square shape and the suspensorium becomes relatively lower than in the nototheniids (Figs 5c, 6c).

The presence of relatively large and numerous teeth on jaws of *Psilodraco* at 14.5 mm SL should be noted which agrees with the data of North (1990) on the early appearance of jaw teeth in this species.

A peculiar character of *P. georgianus* is the presence of few (2-7) small teeth on the ectopterygoid in all studied specimens. In one of the adults, 3 small teeth have also been found on this bone. Among the notothenioids, teeth on the ectopterygoid occur only in *Pseudaphrithis urvilli*, that was considered a plesiomorph feature (Voskoboinikova, 1986; Balushkin, 1992). However, the presence of the ectopterygoid teeth in *P. georgianus* is probably the result of a reversion, because the teeth are few and small. Moreover, possibly it relates to the peculiarity of development of the pterygoids in *Parachaenichthys* and *Gerlachea*. In these genera, the ectopterygoid only appears and it forms the small posterior process instead of the mesopterygoid.

A peculiarity of the development of *Psilodraco* is the presence of numerous small spines along the edges of all the opercular bones at early stages (23.8 mm SL), which gradually disappear in larger specimens. The spines on the suboperculum remain for a longer period, and their shape and position are very similar to those in adults of *Acanthodraco dewitti* (Skora, 1995; Voskoboinikova & Skora, 1996).

At the pectoral fin, the dorsal thorn-like process of the cleithrum, which appears in all four species at the early stages, gradually diminishes during ontogeny to a half of the dorsal lobe of this bone in *Prionodraco*, and disappears in *Parachaenichthys* (Fig. 3).

A remarkable autapomorphy of *Prionodraco* is the presence of two rows of bony plates provided with thorns on their body. The plates probably originate from modified ctenoid scales. In the smallest specimen (20.0 mm SL), each plate bears two thorns, the anterior one being much larger than the posterior (Fig. 7). Later, anterior and posterior thorns become similar in size; then the posterior thorn increases and changes the direction from vertical to posterior. The anterior thorn gradually reduces and disappears. Possibly, the well-developed, laterally directed thorns facilitate the swimming abilities of the larvae; at transition to demersal mode of life, the change of the direction of thorns to posterior also gives some hydrodynamic advantage.

Rate of the osteological development. It is clear from the Tables 1-3 that the appearance of most bony elements is completed in *P. breviceps* at 37 mm, in *P. evansii* at 41 mm, in *P. georgianus* at 47 mm, and in *P. charcoti* at 47 mm. Comparison of the original and literary data on the development of larvae and juveniles of four studied species of the bathydraconids (Kellermann, 1990; North, 1990, 1991) suggests that all species are characterized by more or less full set of bones at the metamorphosis. A similar phenomenon has been found in the nototheniids (Voskoboinikova, 1994). The comparison of sizes of larvae of the nototheniids (Voskoboinikova, 1994; Voskoboinikova & Kellermann, 1997), bathydraconids and channichthyids (Voskoboinikova, 1997) shows that the bathydraconid larval sizes in general are intermediate between those of the nototheniids and channichthyids. Earlier, it was found that the relatively large size of larvae of the nototheniids relates to the slow differentiation of bony skeleton decreasing in advanced species (Voskoboinikova, 1994). Probably, the differentiation of skeleton in the bathydraconids is slower than in the nototheniids, but faster than in the channichthyids. Such reduction of the rate of differentiation was considered a retardation indicating paedomorph character of evolution of the nototheniids (Voskoboinikova, 1994). Comparing the rates of differentiation of skeleton in the three examined families of the notothenioids, we may presume paedomorph evolution in the whole the suborder Notothenioidei.

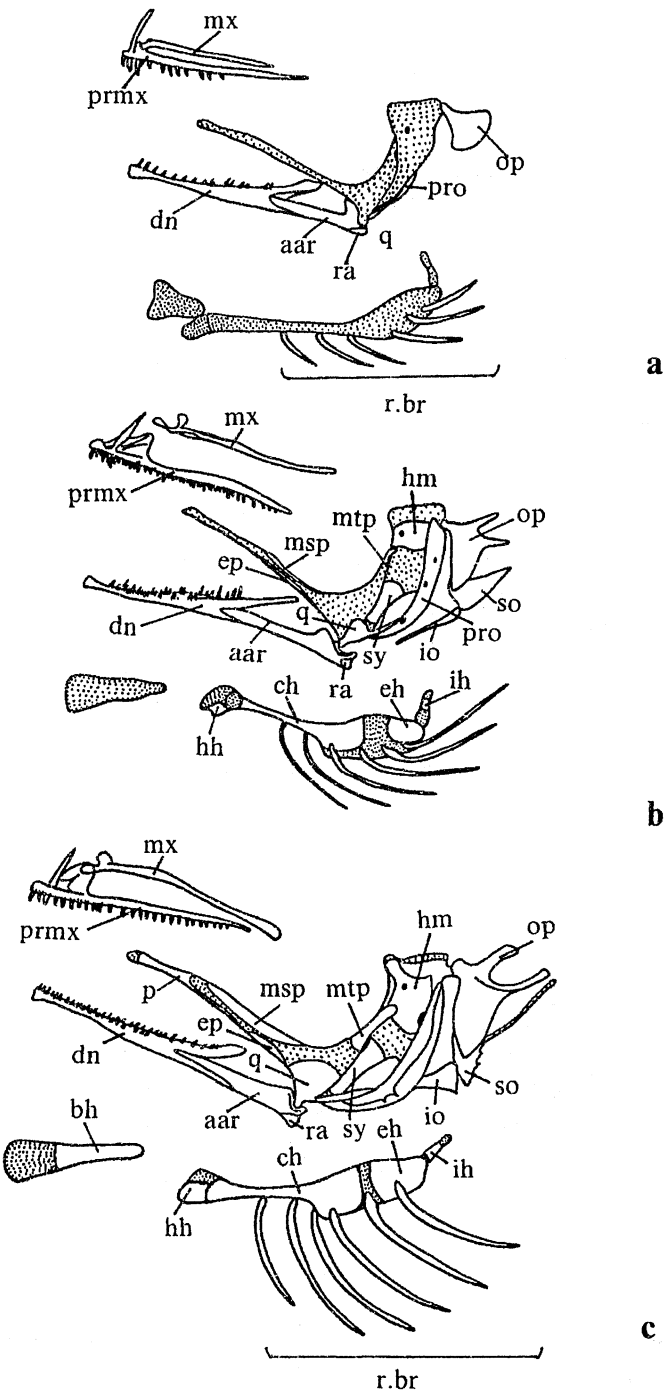

Fig. 5. Development of the splanchnocranium of *Psilodraco breviceps*. Lengths as in Fig. 1. Scale bar 1 mm. *aar*, anguloarticular; *bh*, basihyal; *ch*, ceratohyal; *eh*, epihyal; *ep*, ectopterygoid; *dn*, dentary; *hh*, hypohyal; *hm*, hyomandibular; *ih*, interhyal; *io*, interopercle; *msp*, mesopterygoid; *mtp*, metapterygoid; *mx*, maxilla; *op*, opercle; *p*, palatine; *prmx*, premaxilla; *pro*, preopercle; *q*, quadrate; *ra*, retroarticular; *r.br*, branchiostegal rays; *so*, subopercle; *sy*, symplectic; *ur*, urohyal.

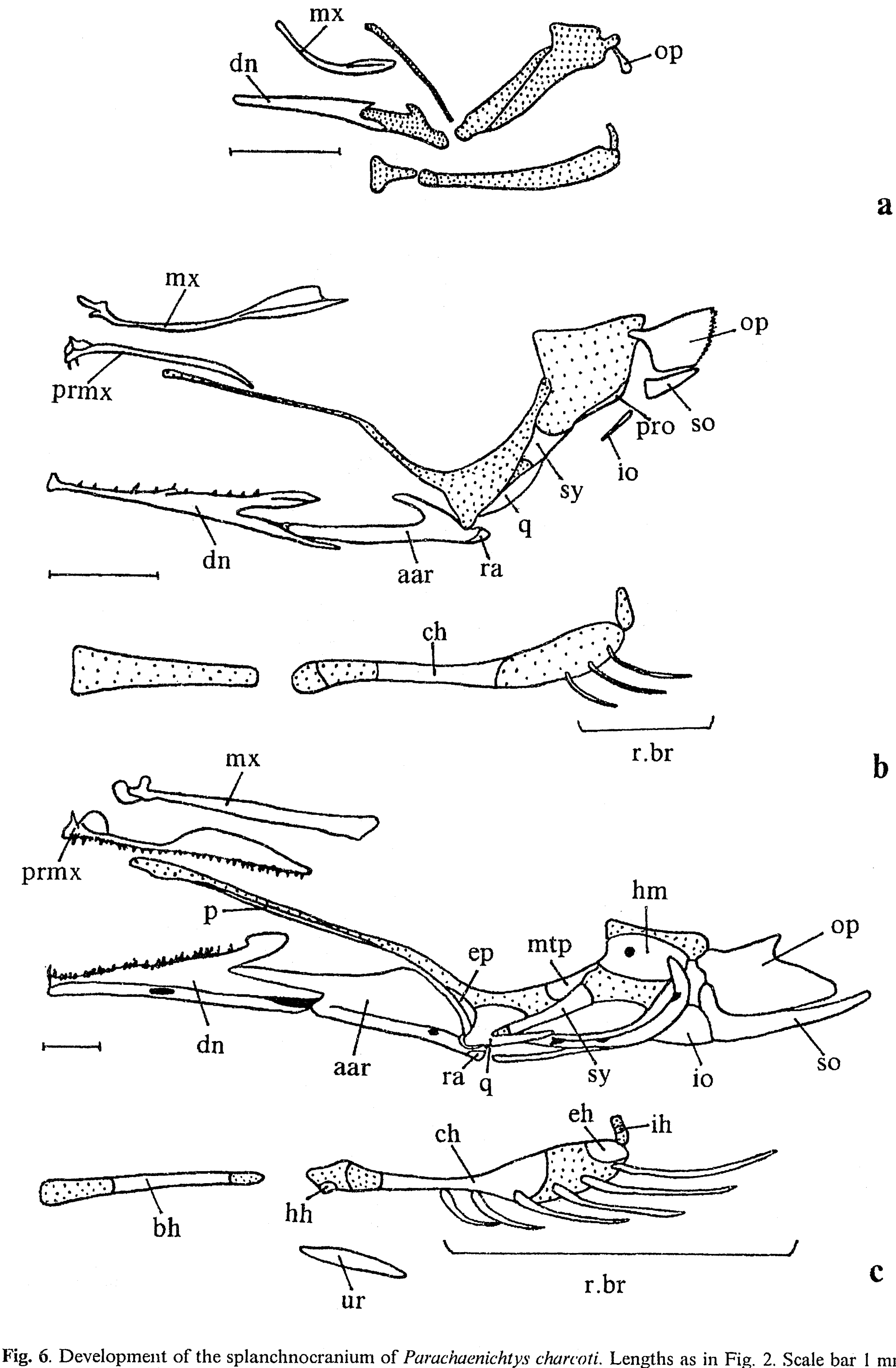

Fig. 6. Development of the splanchnocranium of *Parachaenichtys charcoti*. Lengths as in Fig. 2. Scale bar 1 mm. Abbreviations as in Fig. 5.

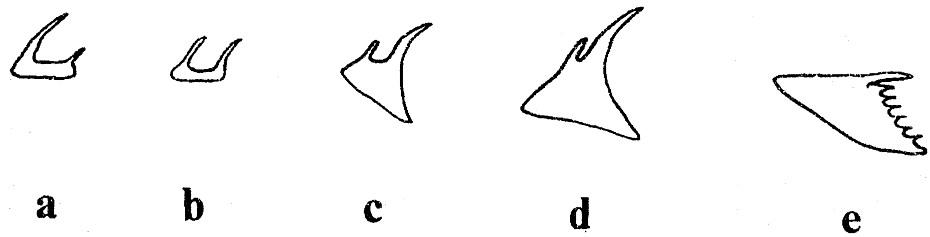

Fig. 7. Development of the body bony plate of *Prionodraco evansii*. Lengths of specimens are (a) 20.5 mm; (b) 24.5 mm; (c) 36.5 mm; (d) 47.5 mm; (e) 151.6 mm.

It would be also interesting to compare the rate of the osteological development within the bathydraconids, which is now impossible due to the absence of precise data on the age of larvae.

Discussion

The investigation of the osteological development of the bathydraconids shows significant differences between the two genera of the subfamily Bathydraconinae, *Prionodraco* (tribe Bathydraconini) and *Parachaenichthys* (tribe Parachaenichthyini), in the sequence and character of appearance of the ethmoidal bones, in the morphogenesis of the neurocranium, splanchnocranium and pectoral fin.

In previous research on the osteological development of the nototheniids and channichthyids, heterochronies in appearance of bony elements within a family were found to occur very rarely (Voskoboinikova, 1994, 1997). Among the nototheniids, only *P. antarcticum* shows a special character of the appearance of bones leading to essential transformations of the skeletal structure of this species. All the studied channichthyids in general show a similar sequence of appearance of bones without great heterochronies (Voskoboinikova, 1997). Heterochronies in appearance of the ethmoidal bones between *Prionodraco* on the one hand and *Parachaenichthys* and *Gerlachea* on the other hand cause sharp differences in the structure of the ethmoidal region of adults (Voskoboinikova, 1988; Balushkin & Voskoboinikova, 1995). If it will be found that *Cygnodraco mawsoni* shows similar heterochronies in the osteological development, the rank of the tribe Parachaenichthyini should be raised to a subfamily.

Acknowledgements

I thank Dr. H.-J. Hirche, Head of the group of planktonology of the Biological Department of the Alfred Wegener Institute for Polar and Marine Research, and Dr. A. Kellermann for supporting my work in Bremerhaven. My thanks are also to Dr. K. Skora and Dr. T. Linkowsky who provided me the material collected by the late W. Slosarchik. Thanks go to Prof. A.P. Andriashev and Dr. A.V. Balushkin for constructive criticism during preparation of the manuscript. The investigation was supported by grants of the Russian Foundation for Basic Research (RFFI) No. 94-04-12089 and of the Deutsche Forschungsgemeinschaft.

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Received 25 December 1997